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Chondriomes in *Chara*

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(WITH PLATE 3)

Chondriomes and mitachondria have received much attention in recent years. Foremost among the investigators along this line are Guilliermond, who has published a number of short papers, and Mottier (14). Both of these writers agree that chondriomes are distinct organs of the cells, and that they arise only from older chondriomes. These cell organs in *Chara* have been described as granulations that stain like nucleoli by Kaiser (11) and by Johow (10). Debski (3, 4) found in the plasma of *Chara* bodies of a nucleolar structure, which probably arose from the nucleolus, and which showed strange enterings on the spindle fibers. Mirande (12), who has given this subject special attention recently, states that in the cells of *Chara* are found certain corpuscles that take the stains like nucleoli. He concludes that most of these corpuscles, which continue to multiply in the cytoplasm, are really nuclear in nature and are in part expelled by the nucleus itself. In the same paper he says that the chondriomes close to the nucleus migrate to the periphery of the cells, develop central vacuoles, and become chloroplasts. In due time he finds that they produce grains of starch.

For the investigation of the origin of these chondriomes in *Chara* and the rôle they play in the cells, material was collected near Covington, Kentucky, and identified according to Robinson

(15) as *Chara fragilis*. A study was also made of *Chara verrucosa*, collected at Oberlin, Ohio.

METHODS

A number of killing agents were employed, including Carnoy's, Jeffrey's, Flemming's, Merkel's, Benda's, and dilutions of a 1 per cent chrom-acetic stock solution. The best results were obtained with Flemming's, Benda's and Merkel's solutions, all of which belong to the group recommended by Guilliermond (8) as causing the least change from the living condition. Care must be used while fixing the material because the chondriomes are rather easily destroyed by strong reagents. Flemming's weaker solution was tried at 0° C. and 50° C., but the best results were secured when the killing agent was of the same temperature as the water in which the *Chara* grew. Sections were cut at 5 μ and 7 μ , and stained with Haidenhain's iron-alum haematoxylin or Flemming's triple stain. Such stains as Giemsa's, Leishman's, and Wright's (Mallory and Wright) were also tried. These possess a certain value for this type of work because of the differential qualities and the rapidity of the staining, but they are likely to cause artefacts due to the precipitation of the stain. The lack of permanence of these stains is a further disadvantage.

Division figures are not easy to secure. Preliminary tests, in which growing tips were killed at intervals throughout the twenty-four hours, showed that mitotic division was most active at ten o'clock at night, and so for the final results the material was killed at this hour.

RESULTS

Since it is during the nuclear division that these chondriomes have their origin, it is necessary to study all the mitotic stages beginning with the resting cell.

While the cell is in the resting stage, the nucleolus shows refractive spots or granules. A similar appearance has been reported by Digby (5) and others in a variety of plants. As the spireme is formed, the nucleolus becomes irregular in shape, while it seems that streams of its contents flow out into the spiral thread (FIGS. 1 and 2). Mottier (13), while writing about nucleolar observations, says it is reasonable to suppose that the

nucleolar substance contributes materially to the growth of the chromosomes. On the same subject Andrews (1) says, "it is probably utilized as food in the growth of chromatic masses." Duggar (6) found an interesting connection between the chromatin content and the nucleolus, while Gardner (7) writes that the nucleolus is the important chromatic center, and that during division it becomes transformed into chromosomes. Wager (17) reports that during spireme formation the nucleolus becomes irregular in shape, undergoes ameboid changes of form, and then disappears just before the formation of the chromosomes. This describes exactly the changes that were observed in the present study of the growing tips.

In the metaphase and following stages the chromosomes remain entirely intact (FIG. 3). There is no sign of disintegration either of the central or outer portions. Hegner (9), working on the paedogenetic larvae of *Miastor*, finds that when the somatic cells become differentiated the middle portions of the chromosomes break up into granules which divide and go to the poles, while the swollen ends are cast into the cytoplasm. Boveri (2) has shown in *Ascaris* that when the cells specialize portions of the chromosomes separate off and disintegrate. But nothing of this kind occurs in *Chara*. Here the chromosomes migrate to the poles in the usual manner, with the mantle fibers extending from the center of the chromosomes. In the anaphase sixteen chromosomes move to each pole, corroborating the count of sixteen to eighteen made by Strasburger (16).

In the region of the median plate, after the chromosomes have been drawn away, a varying number (twelve to sixteen in *C. fragilis* and in *C. verrucosa* even more) of chromatic granules are found (FIG. 4), which are more or less globular in shape and which take the stains just as the chromosomes do. These granules, which are called prochondriomes hereafter, seem to lie between the spindle fibers and do not make connection with the mantle fibers. In size they vary from $0.6\ \mu$ to $1.4\ \mu$ in diameter, and the volume is calculated to be from $0.117\ \text{cu.}\ \mu$ to $1.47\ \text{cu.}\ \mu$. As the chromosomes merge together in the telophase, these prochondriome granules may fuse so as to form eight or ten larger granules (FIG. 5), some of which may be up to $2.5\ \mu$ in diameter, or 4.9

cu. μ in estimated volume. The chromosomes are 0.7μ in thickness and $5-6 \mu$ in length, which gives a calculated volume of 2.37 cu. μ . It is estimated that the amount of chromatic material left behind in some cases may be equivalent to six or eight chromosomes, or almost half the amount of chromatin that makes up one of the daughter nuclei.

At the poles the chromosomes do not fuse directly into the daughter nucleus, but groups of them form pre-nuclear masses (Fig. 5), each of which contains a deeply stained chromatic spot resembling a nucleolus surrounded by a clear area. Then these pre-nuclear masses rapidly fuse into one large daughter nucleus (FIGS. 5-7).

The prochondriomes still persist on the median plate during the formation of the daughter nuclei. They do not disintegrate but soon migrate into the cytoplasm, where they divide repeatedly by fission to form bodies of different sizes. These are the granulations or chondriomes described by Mirande. Thus it appears that the greater number, at least, of the bodies staining as chondriomes in *Chara* may be nuclear in nature, and are, in part, expelled by the nucleus itself. On the other hand, this idea is exactly contrary to that of Guilliermond and Mottier, who say that chondriomes in general arise only from other chondriomes. Meves and Mottier suggest that, because chondriomes are such definite organs of the cell, they may be the bearers of certain hereditary qualities.

The leaves of *Chara* are formed by successive divisions of the tip cell. This tip cell seems to contain more of the chondriomes than any of the other cells. In fact the amount of chondriome material in the tip cells of the young leaves is approximately equal in many cases to the chondriome material in all cells below it. There is thus a progressive accumulation of chondriome material in the tip leaf cell during the successive divisions.

It is impossible actually to trace these prochondriomes to their position on the central plate, for they cannot be definitely picked out among the tangle of chromosomes in the metaphase. No more can their exact origin be seen. It would seem that they may be either (a) delayed chromosomes, (b) entire chromosomes which never go to the poles, (c) portions of chromosomes which

have been cut off, (d) unorganized portions of the spireme, or (e) chromatic material apart from and not included in the spireme. These possibilities are considered in order.

(a) If the original granules which first appear in the anaphase were delayed chromosomes, they would be considerably larger in size and greater in volume and would more nearly resemble the characteristic sausage shape of the chromosomes. Then, too, they would join the other chromosomes at the poles before the daughter nuclei were so nearly formed.

(b) Should they be chromosomes (in spite of their differences in size, shape and volume) which never go to the poles, there would be a progressive reduction in the number of chromosomes in the younger cells. Such, however, is not the case. Eight counts in different parts of the growing tip all gave sixteen as the constant chromosome number.

(c) They are not likely to be cut off portions of chromosomes, because in this event, the chromosomes in the cells which had undergone division a number of times would probably show a progressive diminution in size. According to Boveri (2) and Hegner (9) such diminution occurs in *Ascaris* and *Miastor*, where portions of the chromosomes are cut off at the time when somatic and germ cells are differentiated. In these cases the workers have shown that there is nuclear degeneration attendant on the specialization of the cells. However, nothing of this kind occurs in *Chara*. A careful comparison of the purely vegetative cells and those that might produce gametes, following the morphology according to Goebel, showed that there was no difference in the comparative size or number of the chromosomes or in the number of chondriomes produced.

(d) Unorganized portions of the spireme might form a few such prochondriomes. But there could not be so many unorganized portions as there are prochondriomes in the anaphase and still leave enough material for the full number of chromosomes which are formed.

ORIGIN OF THE PROCHONDRIOMES

(e) There is only one possibility of the origin of these prochondriomes which is not confronted with very serious objections. Since they probably are not chromosomes or portions of chromo-

somes, and do not seem to be unorganized portions of the spireme, they must be chromatin material not included in the spireme. The nucleolus is the most likely container of such material. In the resting stage the refractive spots or granules which may be seen in the nucleolus seem a probable source, because they resemble the prochondriomes in shape and staining reactions. It is possible that, if the nucleolus contains most of the chromatin which goes to make up the chromosomes, it could contain also the amount necessary to make the prochondriomes. Probably some of the granules of the resting nucleolus fail to pass into the spireme, when it is formed from some of the nucleolar material, and are then caught in the tangle of chromosome movement and carried on to the median plate. There they are left because of some difference between them and the granules of the chromosomes.

SUMMARY

1. Chromatic granules (prochondriomes) appear on the central plate in the anaphase of *Chara*; these do not disintegrate but migrate into the cytoplasm and become chondriomes.
2. These prochondriomes have their origin in the nucleolus.
3. Chondriomes are derived by fission from other chondriomes, but they are also produced as nuclear extrusions.
4. No difference in the prochondriome contents has been observed in the actively growing tip between the purely vegetative cells and those which may produce gametes.
5. The extrusion of these prochondriomes is apparently not connected with nuclear degeneration or differentiation of the germ and vegetative cells.

In conclusion the author wishes to acknowledge his obligation to Dr. Harris M. Benedict, of the University of Cincinnati, for his kind supervision during the investigation, to Professor F. O. Grover, of Oberlin College, for helpful suggestions, and also to other friends for the encouragement of their interest.

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Explanation of plate 3

The figures were drawn with a Bausch and Lomb 1.9 objective and ocular 10, tube length 160 mm., with a camera lucida. The slides, from which the figures were drawn, were stained with Flemming's triple stain. The magnification is about 1300 diameters.

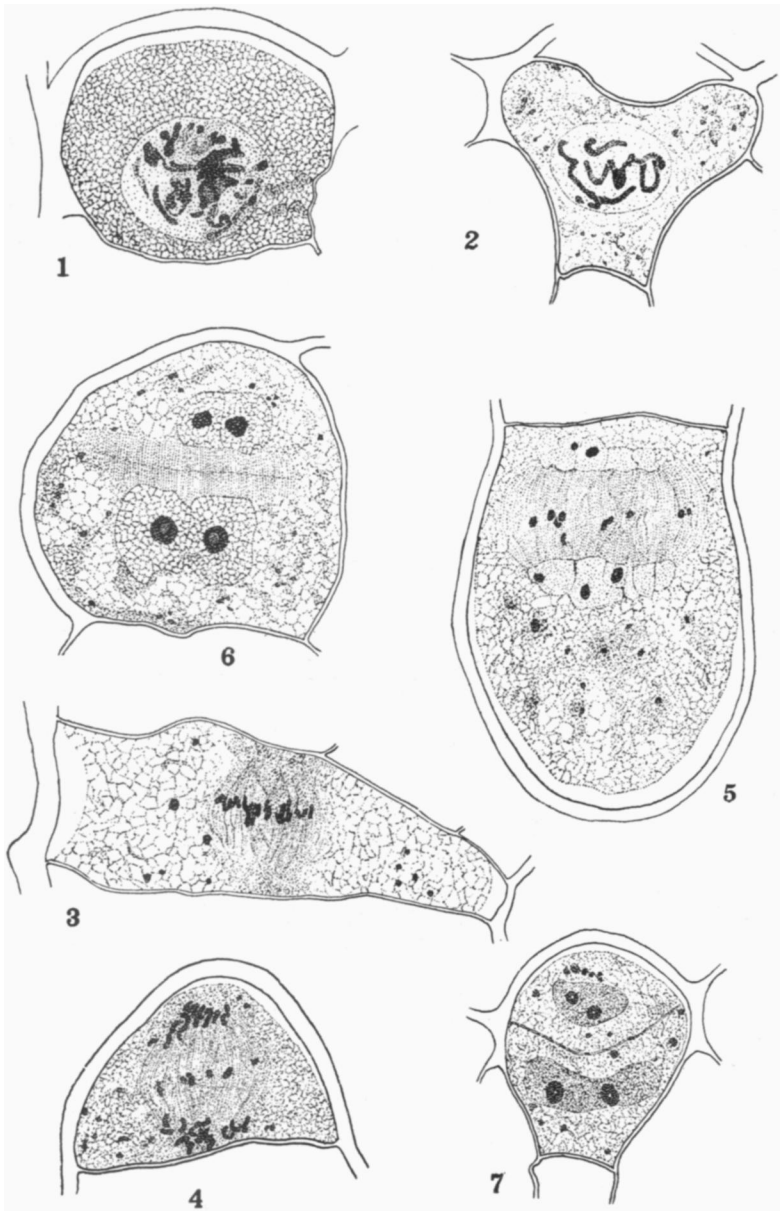
FIGS. 1, 2. Prophase. The nucleolus contributes to the formation of the spireme

FIG. 3. Metaphase. The chromosomes are intact and show no sign of disintegration.

FIG. 4. Telophase. Chromatic granules (prochondriomes) are left on the median plate.

FIG. 5. Late telophase. The prochondriomes still persist during the organization of the chromosomes into prenuclear masses. (The total number of prochondriomes in the section is shown.)

FIGS. 6, 7. Late telophase. The prochondriomes migrate into the cytoplasm as the new wall is formed.



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